ACTIVITY AND WANDERING IN TACHYPODOIULUS NIGER *(LEACH) AND* SCHIZOPHYLLUM SABULOSUM *(L.)*

by

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Introduction

The Schizophylline millipedes, *Tachypodoiulus niger* (Leach) (*T. albipes* C. L. Koch.) and *Schizophyllum sabulosum* (L.), stand apart as being more eurytopic than most Iulids. They also differ in having a succession of mature male stadia, which is made possible by the peculiar phenomenon of periodomorphosis. This was first discovered by Verhoeff (1893) and more recently documented by Halkka (1958) and Sahli (1966).

Blower and Fairhurst (1968) argued that the contribution of successive broods to population increase is probably not very great. Thus, they suggested that the succession of broods, made possible by a series of mature stadia in *Tachypodoiulus niger*, adapts the species to its eurytopic life. It would appear that the Schizophyllinae, in general, have life history characteristics which adapt them for their wanderings.

Perttunen (1953) and Barlow (1957) refer to some behavioural and physiological qualities which adapt the Schizophyllinae to their vagile way of life. They demonstrated that, in the active season, *Schizophyllum* is far more resistant to desiccation and showed that the usual humidity preference is reversed. It was natural to expect that *Tachypodoiulus niger* might have similar adaptations. Fairhurst (1968) has demonstrated this to be true.

In this paper, I wish to present some of the data I have collected on the behaviour and ecology of the two British Schizophyllines. In particular, I shall document the adaptations to relative humidity more fully and examine some aspects of sand-dune activity.

Distribution

Some millipedes have definite habitat preferences. Others, like the Schizophyllinae, are less restricted and their habitats harder to define. Fairhurst (1968) has attempted to explain the distribution with reference to their considerable surface activity. This is a property which appears to be a function of their leg dimensions. Manton (1854) has indicated that *Tachypodoiulus niger*

might have exceeded the maximum leg length compatible with easy burrowing. The same might apply to *Schizophyllum*. If this is so, the habitat must provide effective daytime and winter refuge, in terms of a substrate easy to burrow into. This hypothesis is lent support by the fact that these millipedes are found most abundantly where, for example, there is considerable ground debris, in screes and in sandy areas.

For most other Iulids this wide ranging behaviour would be hazardous with respect to water loss, but *Schizophyllum* and *Tachypodoiulus* are relatively competant in this respect. Variation in survival with season in *Schizophyllum*, was shown by PERTTUNEN and BARLOW. I have demonstrated a similar increase in resistance to water loss, during the active season, for *Tachypodoiulus* (FAIRHURST, 1968).

Responses to environmental factors

We would expect eurytopic species to exhibit several behavioural features, which other species seldom or never show. Recently, I have attempted to survey the main behavioural responses of Schizophylline millipedes, both in the field and in the laboratory. After pilot experiments, using various methods to record activity, such as balanced arenas and interrupted light beams, it was decided that the time lapse camera would most effectively replace human observation. The films used allowed an exposure every $^1/_4$ hour for 4 $^1/_2$ days. Electronic flash illumination, of less than L/1000th of a second duration, was used for each exposure. This did not appear to affect the animals. One of the great advantages of this apparatus, is in the permanent photographic record, to which subsequent reference can be made, should any new behavioural pattern become apparent and require analysis.

Often, in the literature, experiments have been carried out on night-active animals, usually during the day and immediately after they have handled. Furthermore, these experiments have been of very short duration and the observations have not continued into the night. How much information do these experiments produce ? Will the choice of recently handled animals in the daytime, resemble that of a night active animal coming to rest at dawn ? Also, it is reasonable to assume that habitat preferences might differ between the active night phase and the relatively inactive light phase. I suggest that the greatest caution should be exercised in the evaluation of such experiments.

These criticisms may be applied to the work of PERTTUNEN and BARLOW, on the humidity preference of *Schizophyllum* and thus a repetition of some of these experiments was thought desirable. However, long term experiments, with the time lapse camera, have not demonstrated any appreciable difference in selection, between night and day humidity preferences. It may thus be concluded that the results of PERTTUNEN and BARLOW are reasonably accurate and that *Schizophyllum* has a preference for 0 per cent relative humidity in the active season and for 100 per cent in the inactive season.

For *Tachypodoiulus niger*, similar experiments have indicated that the directed response to humidity gradients is abandoned in the active season, rather than reversed. Again, there appears to be no difference in selection, between night and day periods.

I suggest that humidity and other environmental responses change to allow for maximum association for breeding and then dispersal.

Seasonal activity and wandering

The active season for *Schizophyllum sabulosum* is usually May to July. For *Tachypodoiulus niger*, there is normally a spring peak, and there may also be another peak in September and October.

I have studied the ' natural ' wanderings that occur in ' home sites ', that is, sites where the young stages are fully represented. However, in this paper, I wish to refer to activity in habitats which appear to be grossly unsuitable. Such phenomena have occured on a sufficiently large scale, to prompt reports in the literature. Summaries have been published by Schubart (1940), Cloudsley-Thompson (1949) and Demange (1960). The question arises — why are they in these places, and what could govern their activity ?

A careful examination has been made, at a number of British sites where this type of phenomenon occurs. Material has been collected by hand, by pitfall-trapping and by a method of plot-sampling.

The example of wandering I use here, occurs along part of the Lincolnshire coast. At this site, all stages of *Tachypodoiulus* may be found on the dune ridges, where there is plenty of grass and Sea Buckthorn (*Hippophae rhamnoides*). These home sites appear to act as dispersal centres, and in early spring, many individuals may be found in other habitats, including the beach. It was found, however, that not all the stages are inclined to move out of the home sites. The captures out of one of the pitfall jar transects is illustrated in fig. 1. The salt marsh pool, at one end of the transect was regularly flooded by the tide, up to trap number 4. Traps 5 to 10 were in a Sea Buckthorn area. This region was shown to be a home site by the presence of immature stadia. These do not move into the tidal areas. It was also discovered, that adults do not tend to move out of the home site until they have moulted (in recently moulted animals, the newly added row of ocelli will not become fully pigmented, until at least a week after the moult.). The indications are, that intercalary males may be restricted, in a similar way to the adults, which have not recently moulted. What, however, are the behavioural restrictions placed on intercalary and unmoulted adults ? Experiments are in hand to illuminate this problem. A start has been made, for example a comparison of pitfall-trapping (active population) and plot sampling (total population) on the same site, has shown that *Schizophyllum* copulatory males are nearly six times as active as intercalary males.

Orientation

From general observations, on sand-dune areas, the direction of movement of the millipedes was sufficiently consistent for orientation mechanisms to be suspected.

To test for this, millipedes found on the beach were placed in a circle, of eight feet in diameter, drawn in the sand. This exercise was carried out for both species, at all times of the day and in varying wind conditions. The overall picture (fig. 2) that emerges, is that *Tachypodoiulus* is strongly nega-

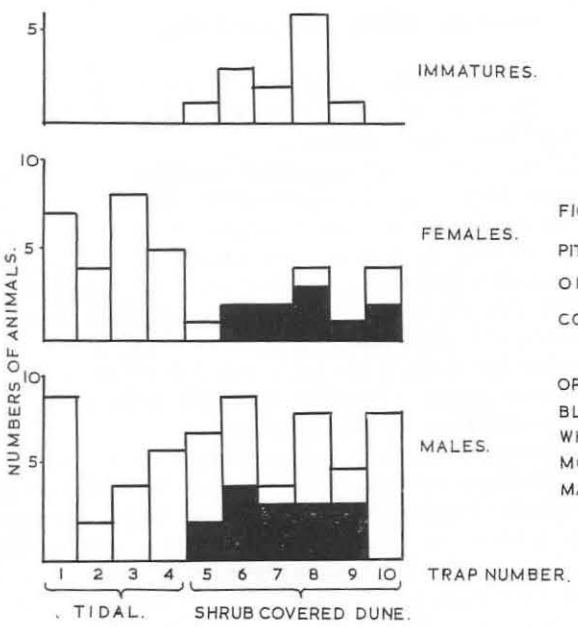

FIG. 1. TACHYPODOIULUS. PITFALL-TRAP CAPTURES ON THE LINCOLN SHIRE COAST.

OPEN COLUMNS ARE TOTALS. BLACK COLUMNS ARE ADULTS WHICH HAVE NOT RECENTLY MOULTED, AND INTERCALARY MALES.

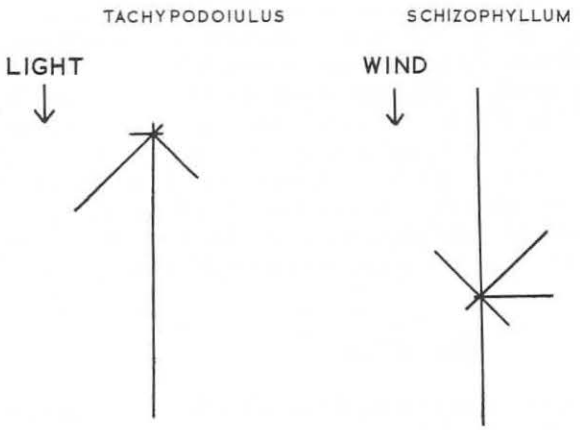

FIG.2 ORIENTATION OF MILLEPEDES ON BEACHES.

THE LENGTHS OF THE LINES REPRESENT THE RELATIVE NUMBERS

tively phototactic. The reaction is the same whether they are exposed to the sun, moon, or even the diffuse light produced by the sun below the horizon. The effect of wind appears to be negligible. In *Schizophyllum*, however, the primary factor in orientation appears to be the wind, although the direction of the sun may have a modifying effect.

We can appreciate that millipedes in open spaces would be inclined to seek darker habitats and that *Schizophyllum*, with its slightly shorter legs, must show more deference to wind. We may now ask — is this orientation merely emergency procedure or is it related to a normal dispersal mechanism ? These orientation factors may indeed be obeyed in the normal night active phase and there is a definite survival value in having a group, rather than an individual reaching a new habitat.

Day-time activity

In open areas, Schizophylline millipedes may often show considerable day-time activity. Edney (1953) mentioned that woodlice may become photopositive in dry air or high temperatures and I have demonstrated a similar reaction in millipedes in the laboratory. One of the advantages of such behaviour is that by evaporation, they may be able to maintain the body temperature below a dangerous level.

The wandering habits may easily force them, at dawn, into refuges which may become unsuitable in the heat of the day. I suggest that day-time activity is an emergency response to such ecological crises.

Summary

Diurnal and seasonal peaks of activity, which culminate in wandering phenomena are characteristic of these two Iulids. Extensive behavioural experiments have been carried out, both in the laboratory and in the field, in order to estimate the influence of the major environmental factors. The results show a degree of independance of habitat which is perhaps not approached by other European millipedes. Behavioural differences between intercalary and copulatory males and orientation mechanisms are discussed, as well as day-time activity. The male periodomorphosis, linked with the behaviour of Schizophylline millipedes appears to produce an efficient dispersal mechanism.

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